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Trithemis morrisoni sp. nov. and *T. palustris* sp. nov. from the Okavango and Upper Zambezi Floodplains previously hidden under *T. stictica* (Odonata: Libellulidae)

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Abstract

During the course of a population genetic study of *Trithemis stictica* that included sites in Namibia, Kenya, Tanzania, Ethiopia, Botswana and Zambia, two undescribed libellulid species were discovered in the Okavango and Upper Zambezi Floodplains. These were both previously identified as *T. stictica*. We describe the two species, *T. morrisoni* sp. nov. (holotype ♂: Namibia, Nature Reserve Popa Falls, Okavango River at the rapids, 18°07′S, 21°40′E; iv 2007, leg. K.-D.B. Dijkstra; dep. in the National Museum of Namibia, Windhoek) and *T. palustris* sp. nov. (holotype ♂: Botswana, Okavango Delta, Moremi Game Reserve, 19°15′S, 23°20′E; ii 2007, leg J. Kipping; dep. in the National Museum of Namibia, Windhoek) and compare them with *T. stictica*.

Introduction

The genus *Trithemis* Brauer is predominately distributed throughout Africa, including its islands, with a small number of species in Asia (Pinhey 1970). Altogether about 40 species are recognised. The species of the genus show a wide variety of habitat preferences, ranging from generalists to range-restricted specialists. Pinhey (1970) revised the genus, concentrating on the African species. Most of his material is kept in the Natural History Museum of Zimbabwe in Bulawayo (NMBZ). Additional taxonomic work was published by Clausnitzer (2001) and by Dijkstra (2007) who recently revisited Pinhey's collection.

Between 2001 and 2005 a field project mapping the odonates of Namibia was conducted (Suhling et al. in press). Distribution patterns and dispersal strategies of several key species were studied with population genetic analyses (Hadrys et al. 2006; Dijkstra et al. 2007; SD, HH unpubl.). At the same time other associated projects provided insights in distribution patterns of the genus in neighbouring countries, e.g. from Botswana with the vast Okavango Delta swamps and its surroundings (Kipping 2003, in press). For population genetic

studies, samples of *T. stictica* (Burmeister, 1839) were collected from 15 localities in Namibia, Botswana, Zambia, South Africa, Kenya, Tanzania and Ethiopia (Fig. 1). While other *Trithemis* species occur throughout Namibia, *T. stictica* was exclusively found at isolated springs in the Naukluft Mountains and in the region of the Caprivi Strip with its surrounding river systems in Botswana and Zambia (Kipping in press; Suhling & Martens 2007). In other sub-Saharan African countries the species is common and inhabits swamps, pools or streams in open areas (Pinhey 1970).

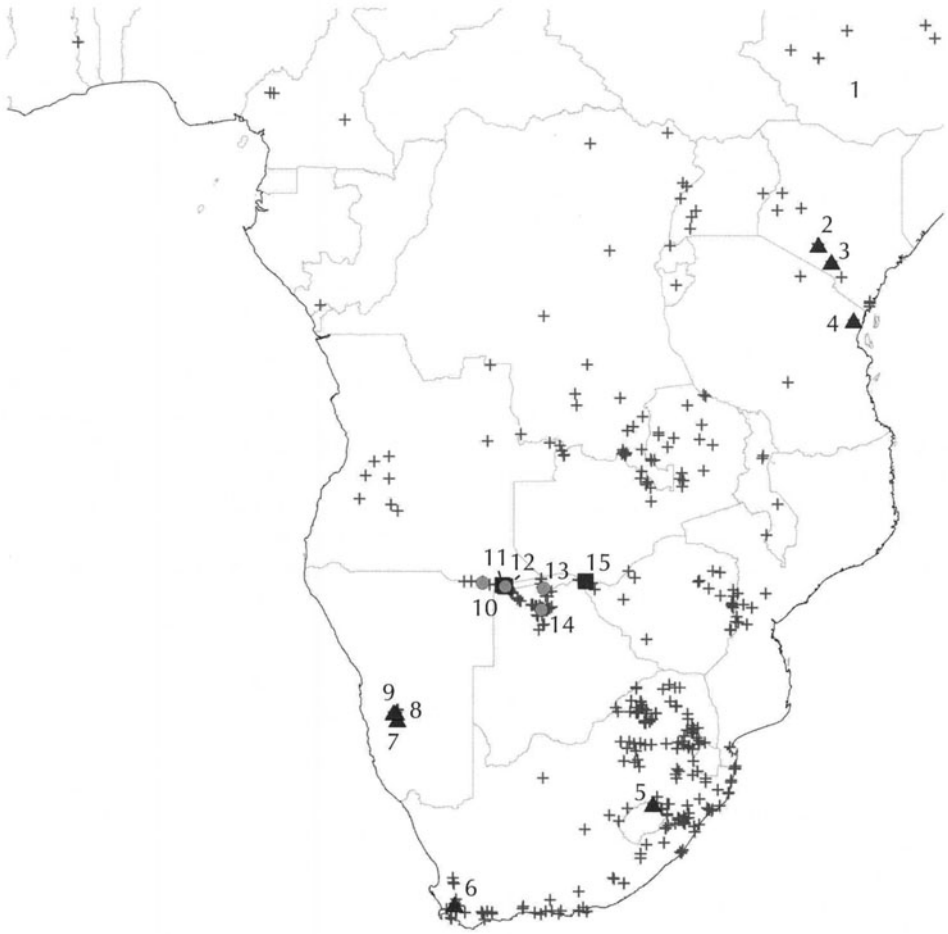

Figure 1: Distribution map of the *Trithemis stictica* group — *T. morrisoni* sp. nov. (■), *T. palustris* sp. nov. (●) and *T. stictica* (▲). (+) displays all records of the group (one of the three above species) which were not identified so far. Sites of analysed populations – 1: Ethiopia; 2: Nairobi NP, Kenya; 3: Kiboko River, Kenya; 4: Usambara Mt., Tanzania; 5: Royal Natal Park, RSA; 6: Western Cape, RSA; 7: Naukluft Mt. Tsams Ost, Namibia; 8: Naukluft Mt. Naukluft River, Namibia; 9: Naukluft Mt. Zebra River, Namibia; 10: mouth of Omatako River in Okavango River, Namibia; 11: Andara, Okavango River, Namibia; 12: Popa Falls, Okavango River, Namibia; 13: Kwando River, Namibia; 14: Okavango Delta, Botswana; 15: Zambezi River, Zambia.

The population genetic study discovered three distinct and completely reproductively and genetically isolated clades within what had been called *T. stictica* (SD, HH unpubl.[1]). The genetic distances of four genetic markers between the clades are unequivocal at the species level. In a phylogenetic tree comparing several species of the genus *Trithemis*, the two newly discovered species are sister species, but are more distantly related to *T. stictica.* Molecular clock analyses suggest that the split between the two new species occurred about one million years ago (SD, HH unpubl.). Because the discovery of new species based solely on genetic data is controversial and in some cases clearly arguable (e.g. DeSalle et al. 2005; Hickerson et al. 2006), we took an integrative approach to species delimitation which includes morphological, ecological, geographical, and genetic characters (SD, HH unpubl.). In this analysis all evidence leads to the recognition of two new species. Since the phenotypes of the three species are very similar, they were first identified in the field as *T. stictica.* However, detailed morphological analyses revealed significant differences. Here we describe the two new species *T. morrisoni* sp. nov. and *T. palustris* sp. nov. and their morphological differences with *T. stictica.*

Material and methods

Of 106 genetically analysed specimens, 43 males from Kenya, Tanzania, South Africa, Namibia, Botswana, and Zambia covering the three genetic groups were selected for morphological analyses. We examined the external appearance of the specimens: patterns of thorax and abdomen, wing venation, shape of secondary genitalia and appendices, pubescence, coloration of Pt, frons, vertex, eyes and patch of Hw, and we measured 11 phenotypic characters, e.g. the length of the Hw, abdomen and Pt of the Fw with a stereomicroscope, and analysed the male secondary genitalia with a scanning electron microscope (SEM). Statistical tests were performed using SAS, first to test for Normality (Shapiro-Wilk test) and then to analyse the significance of morphological differences between the genetic groups (Wilcoxon test). Additionally we examined seven females representative of each new species.

Trithemis morrisoni sp. nov.

(Figs 1, 2a-d, Plate IIIa)

Trithemis stictica (Burmeister). — Pinhey (1970: 127-128, figs. 47, in part, notes on Victoria Falls dwarf series); — Kipping (2003); — Martens et al. (2003: in part).
Trithemis sp. nov. — Kipping (in press); — Kipping & Suhling (in press); — Suhling et al. (in press); — Suhling & Martens (2007: 233-234, in part).

Etymology

Named after the poet James Douglas Morrison and his passion for deserts and the hidden mysteries of nature.

[1] Three papers have been submitted to be published elsewhere, with the following titles: "Odonata in the desert. Population structure and dynamics in the desert inhabiting dragonfly *Trithemis arteriosa*" – "Speciation via habitat specialisation – a case study in the odonate genus *Trithemis* (Odonata: Libellulidae)" – "An integrative approach for species discovery – from character-based DNA-barcoding to ecology"

Specimens studied

Total number of adult specimens examined: 12 ♂, 7 ♀. — **Holotype** ♂: Namibia, Nature Reserve Popa Falls, Okavango River at the rapids (18°07′S, 21°40′E), iv 2007, leg. K.-D.B. Dijkstra, K. Schütte, V.J. Kalkman; — **Paratypes**: 3 ♂: same data as holotype, iv 2003, leg. S. Damm; 2 ♂: ii 2004, leg. F. Suhling; 3 ♂: Namibia, near Catholic Mission Station Andara, Okavango River (18°01′S, 21°30′E), ii 2004, leg. F. Suhling; 3 ♂, 7 ♀: Zambia, Bovu Island, Zambezi River (17°29′S, 25°20′E), ii 2007, leg J. Kipping. The holotype will be deposited in the National Museum of Namibia, Windhoek. Paratypes will stay at University of Veterinary Medicine Hannover, ITZ, Ecology & Evolution, Germany.

Description of holotype male

Head: Labium yellow with a broad black band in the middle extending onto the posterior lobe and the anterior margins of the lateral lobes. Face yellow. Postclypeus with two central, separated black comma-shaped streaks. Frons and vertex metallic steel-blue. Antennae black. Labrum black with two lateral yellow spots. Occipital triangle black with two yellow posterior spots. Back of the head black with four yellow spots. Eyes bicoloured; brownish-red on the upperside and yellow-grey on the underside.
Thorax: Prothorax black with the anterior collar yellow. Median lobe with two yellow markings. Synthorax showing a light blue pruinosity and more ventrally with less pruinosity, where it becomes yellow and black. Metepimera yellow with only little pruinosity. Legs black, with the inner side of the fore femora yellow. — Wings: venation blackish. Pt brown between blackish veins. Cells at the base of the Fw and Hw amber (up to 2 mm from body). Hw with amber patch starting at the triangle and including the anal loop. In Fw 10½-11½ Ax, in Hw 8 Ax, in Fw 13 Px, in Hw 11 Px. Fw triangle of 2, Hw triangle of 1, subtriangle of 3 cells; supratriangle uncrossed.
Abdomen: Abdomen slender, narrowest at S4 and widest at S8. S1-3 black with broad yellow streaks and ventrally with little blue pruinosity. S4-8 black with sharp yellow streaks on each side. S9 black without any yellow. Dorsum of S10 with a yellow spot in the middle. Appendages black. Anterior lamina and hamule black with pale brown bristles; secondary genitalia surrounded by white hair; for details see Figs 2a-b. Penis of holotype not examined.
Measurements [mm]: Entire length 32.4, abdomen length (excl. appendages) 20.4, Fw length 25.9, Hw length 25.5, Pt (Fw) 3.2, appendages 1.5 mm, S4 3.4 mm.

Variation in males

There is little size variation between males (n = 12): abdomen length 19.9-22.5 mm; Fw length 25.8-26.5 mm; Hw length 23.2-26.8 mm; Pt (Fw) length 3.2-3.7 mm; appendages 1.3-1.6 mm; S4 3.3-3.5 mm. The colour of Pt varied between light and dark brown, with the inner side always a slightly lighter brown. All specimens have the amber patch on Hw except for one specimen from the Zambezi River, where only a trace of amber was found. Two specimens from the Zambezi River show a small yellow spot on S9. The comma-shaped streaks on the postclypeus are absent in five Popa Falls males and in the Zambian specimens. The coloration of thorax and abdomen varied between dark brown and black. In two specimens from the Zambezi River and in five from Popa Falls the yellow is ivory.

Description of female

Described is paratype Tmor140H; 140 is locality code for Bovu Island, specimen H.
Head: Labium yellow with a broad black band in the middle, extending onto the posterior lobe and the anterior margins of the lateral lobes. Face yellow. Postclypeus without any markings. Frons and vertex metallic steel-blue/green. Antennae black. Labrum black with two elliptical lateral yellow spots. Occipital triangle black with two yellow posterior spots. Back of the head black with four yellow spots. Eyes bicoloured; brownish-red on the upperside and yellow-grey on the underside.
Thorax: Prothorax black with a little yellow. Synthorax generally has a black and yellow pattern, with black on the anterior side of mesepimera, metepisterna and metepimera and yellow on the posterior side. Mesepisterna with a central black band and metepisterna with an additional hook-shaped black streak on the ventral side. Legs black, with the inner side of the fore femora yellow. Ventral side black with three yellow spots posteriorly. — Wings: clear with blackish venation. Base of the wings amber including the first cell directly at the body in Fw and Hw. Pt brown between black veins. A trace of amber in the Hw, extends from the triangle, expanding to three cells width and up to and including the anal loop. In Fw 9½-10½ Ax, in Hw 8 Ax, in Fw 12 Px, in Hw 12 Px. Fw triangle of 2, Hw triangle of 1, subtriangle of 2 cells; supratriangle uncrossed.
Abdomen: Abdomen narrowest at S4 and widest at S7, where 2mm wide. S1-3 with yellow and black pattern like in male. S4-8 black with sharp yellow streaks on each side. S9 with a yellow spot at each side. S10 with a short yellow band in the middle.
Measurements [mm]: Entire length 31.6, abdomen length (excl. appendages) 20.5, Fw length 26.3, Hw length 25.0, Pt (Fw) 3.2, S7 2.0 mm.

Variation in females

The size of females (n = 7) varies only little: abdomen length 20.2-21.5 mm; Fw length 25.3-26.5 mm; Hw length 25.0-26.7 mm; Pt (Fw) length 3.2-3.5 mm; S7 1.8-2.1 mm broad. Two specimens have the central amber patch on the Hw, the others not. The basal amber of the wings varies between half to the whole first cell directly at the thorax. Fw with 9½-11½ Ax.

Trithemis palustris sp. nov.

(Figs 1, 2a-c, e, Plates IIIb, IV)

Trithemis stictica (Burmeister). — Pinhey (1970: 126, 128, in part, notes on a Botswana series); — Kipping (2003); — Martens et al. (2003: in part)
Trithemis sp. nov. — Kipping (in press); — Kipping & Suhling (in press); — Suhling et al. (in press) — Suhling & Martens (2007: 233-234, in part).

Etymology

The adjective 'palustris' refers to its habitat, the swampy regions of the Okavango Delta and Kwando River.

Specimens studied

Total number of adult specimens examined: 11 ♂, 7 ♀. — **Holotype** ♂: Botswana, Okavango Delta, Moremi Game Reserve, Third Bridge (19°15′S, 23°20′E), ii 2007, leg J. Kipping;

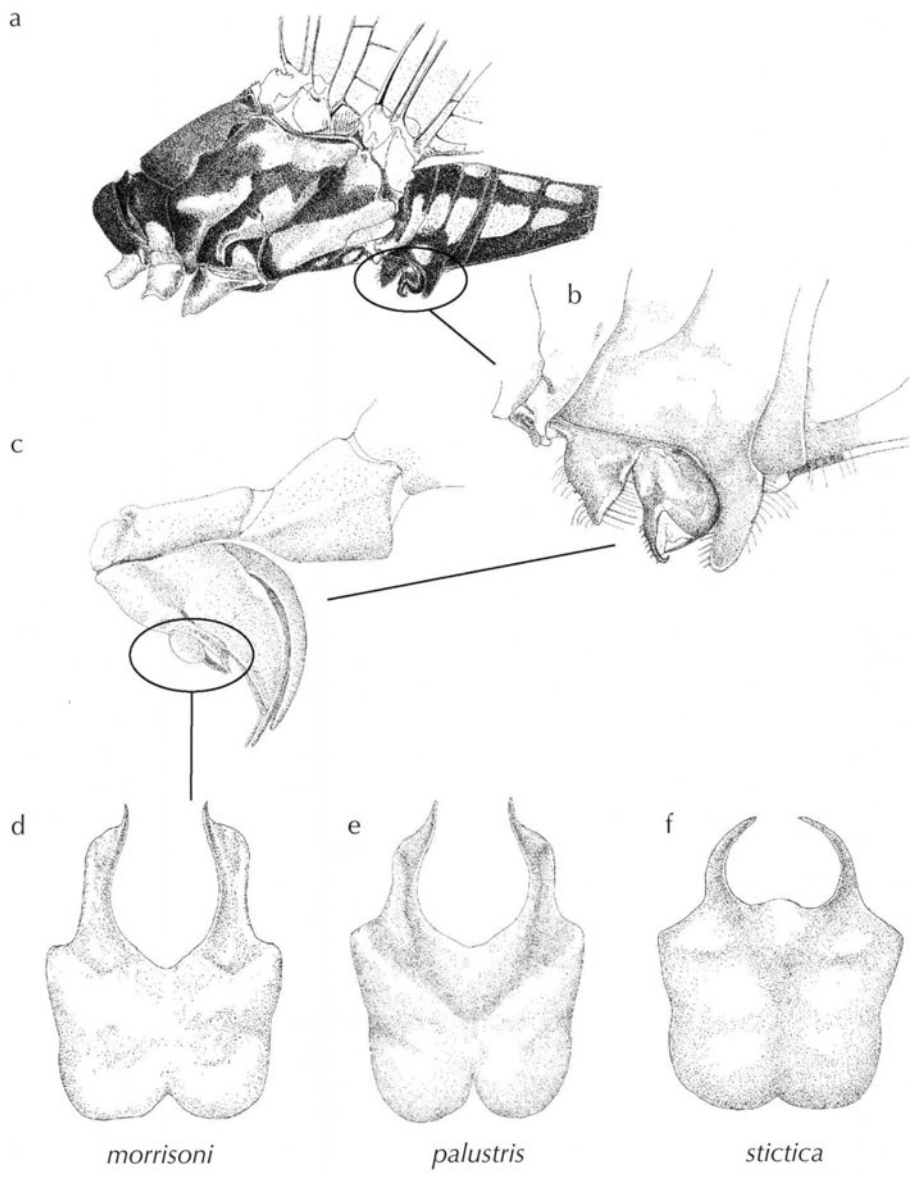

Figure 2: Male characters of *Trithemis morrisoni*, *T. palustris* and *T. stictica* — (a) thorax and S1-3, secondary genitalia only sketched, (b) secondary genitalia, (c) first two segments of the penis, including the distal segment and the lateral view of the "cornuti"; all in left lateral view of *T. palustris* but pattern and structure are the same in all three species; (d-f) comparison of the paired hook-shaped extension of the hood, the "cornuti", of *T. morrisoni* (d), *T. palustris* (e) and *T. stictica* (f).

Paratypes: 2 ♂: Namibia, Nature Reserve Popa Falls, Okavango River at the rapids, iv 2003, leg. S. Damm; 4 ♂: Namibia, Mudumu National Park, Kwando River (18°30′S, 23°32′E), iv 2004, leg. F. Suhling. 1 ♂: Namibia, mouth of Omatako River in Okavango River, ca 50 km E of Rundu (18°00′S, 20°35′E), iv 2004, leg. F. Suhling; 3 ♂, 7 ♀: same as holotype, leg J. Kipping. The holotype will be deposited in the National Museum of Namibia, Windhoek. Paratypes will stay at University of Veterinary Medicine Hannover, ITZ, Ecology & Evolution, Germany.

Description of holotype male

Head: Labium yellow with a broad black band in the middle also covering the posterior lobe and expanding onto anterior margins of lateral lobes. Face creamy yellow, postclypeus with two central, separated black streaks reaching the lower border. Labrum black with two elliptical lateral yellow spots. Frons metallic steel-blue. Antennae black. Occipital triangle black with two yellow posterior spots. Back of the head black with four yellow spots. Eyes with two colours; the upper part brownish red and the lower part grey.
Thorax: Prothorax black with anterior collar yellow. Median lobe with two yellow markings. Synthorax black and yellow dorsally, with light blue pruinosity. Metepimera yellow and black with little pruinosity. Legs black, with the inner side of the fore femora beige. — Wings: venation blackish. Pt brown between blackish veins. Base of the wings slightly yellow/amber. A light amber patch on Hw starting at the triangle covering only a few cells in the direction of the anal loop. In Fw 10½ Ax, in Hw 8 Ax, in Fw 14 Px, in Hw 12 Px. Fw triangle of 2, Hw triangle of 1, subtriangle of 3 cells; supratriangle uncrossed.
Abdomen: Abdomen slender, narrowest at S4 and widest at S8. S1-3 black with yellow pattern and ventrally with some blue pruinosity. S4-8 black with sharp yellow spots on each side. S9 black without any yellow. Dorsum of S10 with a yellow spot. Appendages black. Anterior lamina and hamule black with pale brown bristles and white hair around secondary genitalia. For details see Figures 2a-b. Penis of holotype not examined.
Measurements [mm]: Entire length 34.5, abdomen length (excl. appendages) 23.9, Fw length 27.0, Hw length 26.5, Pt (Fw) 3.2, appendages 1.5 mm, S4 3.8 mm.

Variation in males

Size variation in males (n = 11): abdomen length 22.7-23.8 mm; Fw length 26.5-27.8 mm; Hw length 25.5-27.0 mm; Pt (Fw) length 3.2-3.5 mm; appendages 1.5-1.6 mm; S4 3.7-4.0 mm. Colour of Pt is light brown in the Kwando River specimens, but dark brown in the others. The inner side is a slightly lighter brown. The amber patch on the Hw is absent in two specimens of the Okavango Delta, present in the Popa Falls males and only a trace of amber was found in the other specimens. The coloration of thorax and abdomen varied between dark brown and black.

Description of female

Described is paratype Tpal141F; 141: locality code Moremi Game Reserve, specimen F.
Head: Labium yellow with a broad black band in the middle extending onto the posterior lobe and the anterior margins of the lateral lobes. Face yellow. Postclypeus with two central comma-shaped streaks extending to the lower margins of the postclypeus. Frons and vertex metallic steel-blue/green. Antennae black. Labrum black with two elliptical lateral

yellow spots. Occipital triangle black with two yellow posterior spots. Back of the head black with four yellow spots. Eyes with two colours; the upper part brown-red and the lower part grey.

Thorax: Prothorax black with yellow pattern. Synthorax yellow with black markings. Mesepisterna with a black streak in the middle; mesepimera, metepisterna and metepimera with a black streak on the anterior margin. Metepisterna additionally with a hook-shaped black streak ventrally. Legs black with the fore femora yellow on the inner side. Ventral side black with three yellow spots posteriorly. — Wings: venation blackish and Pt brown between black veins. Bases of the wings amber including half of the first cell directly at the thorax in Fw and Hw. Wing tips of Fw and Hw brownish, which also includes Pt. In Fw 10½-11½ Ax, in Hw 8 Ax, in Fw 13 Px, in Hw 13 Px. Fw triangle of 2, Hw triangle of 1, subtriangle of 3 cells; supratriangle uncrossed.

Abdomen: S4-10 thicker than in males, narrowest at S4; S7 1.7 mm broad. S1-3 with yellow and black pattern like in males. S4-8 are black with sharp yellow streaks on each side. S10 with a short yellow dorsal band in the middle.

Measurements [mm]: Entire length 33.8, abdomen length (excl. appendages) 24.5, Fw length 27.5, Hw length 26.3, Pt (Fw) 3.2, S7 1.5 mm.

Variation in females

Size variation in females ($n = 7$): abdomen length 23.5-24.0 mm; Fw length 26.0-27.8 mm; Hw length 25.3-26.9 mm; Pt (Fw) length 3.1-3.5 mm; S7 1.4-1.7 mm broad. Most obvious is the variation in intensity and size of the infuscated area of the wing tips. The brownish coloration reaches up to the distal end of Pt in two specimens, in which the coloration is very intensive, and also three costal cells distal of the nodus are brownish. One specimen lacks darkened tips, and another has only a trace of brown at the extreme tip. Number of Fw Ax varied from 9½ to 11½ Ax.

Trithemis stictica (Burmeister, 1839)

(Figs 1, 2a-c, f)

Libellula stictica Burmeister, 1839: 850 (loc. typ. "Port natal" = Durban, RSA).
Trithemis stictica (Burmeister). — Brauer (1868).
Trithemis parasticta Pinhey, 1956: 35-37, fig. 8a (loc. typ. Lake Chila, Abercorn, Zambia);
— Lieftinck (1969: 52-53, "a very near ally to *T. stictica*", comparison of both species);
— Pinhey (1970: 125, 129, "only a minor largish, dark variety", synonymy).
Trithemis stictica dwarfs, forms, subspecies — Pinhey (1970: 129, equatorial subspecies).

Specimens studied

Total number of adult specimens: 20 ♂. — 3 ♂: Namibia, Namib Naukluft Reserve, Tsaris Mountains, Zebra River (24°35′S, 16°20′E), iii 2003, leg. S. Damm; 2 ♂: Namibia, Namib Naukluft Reserve, Naukluft Mountains, Tsams Ost (24°15′S, 16°06′E) iv 2004, leg. F. Suhling; 4 ♂: Tanzania, East Usambara Mountains (5°05′S, 38°37′E), x 2002, leg. V. Clausnitzer; 1 ♂: Kenya, Nairobi National Park (1°25′S, 36°55′E), ix 2002, leg. V. Clausnitzer; - 5 ♂: Kenya, Kiboko River (2°15′S, 37°32′E), ix 2002, leg. V. Clausnitzer; 3 ♂: South Africa, Royal Natal Park (28°41′S, 28°48′E), 2001, leg. J. Ott; 2 ♂: RSA, Western Cape, Hawekwas Mts, Bains Kloof (33°55′S, 19°09′E), i 2006, leg. K.-D. B. Dijkstra.

Redescription of male

Described is reference male Tst 118D; 118: locality code Zebra River, Namibia, specimen D.
Head: Labium yellow with a broad black band in the middle, covering the posterior lobe and expanding to the anterior margins of lateral lobes. Labrum black with two yellow lateral spots. Frons and vertex steely blue. Face creamy yellow. Postclypeus with two central, separated, black comma-shaped streaks. Antennae black. Occipital triangle black with two yellow posterior spots. Back of the head black with four yellow spots. Upperside of eyes light red grading to light grey on the underside: the colours thus not sharply demarcated.
Thorax: Prothorax black with slight yellow markings. Synthorax except ventrally with blue pruinosity. Ventral side with yellow and black patterns. Metepimera with less pruinosity. Here yellow with the anterior side black. Legs black with the inner side of fore femora light brown. — Wings: clear with dark brown venation. Pt brown, grading to light brown on proximal side, between dark brown veins. Light amber area starting at the triangle and covering the anal loop of Hw. In Fw 9½-10½ Ax, in Hw 8 Ax, in Fw 13 Px, in Hw 12 Px. Fw triangle of 2, Hw triangle of 1, subtriangle of 2 cells; supratriangle uncrossed.
Abdomen: Slender with S4 narrowest. S1 black dorsally and yellow ventrally. S2 black with two short yellow streaks. S3 black with yellow pattern. S4-8 black with a single row of yellow streaks on each side. S9 with a yellow spot on each side. S10 black with a central dorsal yellow line. Appendages dark brown. Hamule and anterior lamina black and coated on outer side with short thick setae and brown bristles (Figs 2a-b).
Measurements [mm]: Entire length 33.5, abdomen length (excl. appendages) 23.5, Fw length 28.2, Hw length 26.3, Pt (Fw) 3.3, appendages 1.5 mm, S4 3.8 mm.

Variation in males

Size variation in males ($n = 20$): abdomen length 22.1-24.8 mm; Fw length 27.8-30.5 mm; Hw length 26.5-29.5 mm; Pt (Fw) length 3.2-3.8 mm; appendages 1.2-1.7 mm; S4 3.6-4.0 mm. The colour of the Pt is brown in most of the specimens, but dark brown in the Tanzanian males, with the proximal side slightly lighter brown. The amber patch on Hw is present in all specimens but varying in intensity. The coloration of thorax and abdomen is black and bright yellow in the South African, Tanzanian and Kenyan specimens, but brown with creamy yellow in the Namibian ones. Yellow spot on S9 is present in four of the Namibian males, but absent in the others.

Diagnostic characters of the three taxa

Male morphology

The most obvious character that distinguishes *Trithemis morrisoni* sp. nov. and *T. palustris* sp. nov. from *T. stictica* is the eye coloration (see Plates III, IV). The eyes of *T. morrisoni* and *T. palustris* are red-brown on the upper- and grey-blue on the underside. In mature males of *T. palustris* the red-brown coloration can change to bluish but a brown tinge is always left (see Colour plate IV). In contrast, the eyes of *T. stictica* show no colour separation. A second character is the amber base of the wings that both new species have, but is absent in *T. stictica*.

The trait with the most evidence for speciation is the morphology of the penis. SEM revealed a different shape of the "cornuti" (terminology by Pinhey 1970), the paired hook-shaped extensions of the hood of the distal segment of the penis (Figs 2d-f). In *T. stictica*

Table 1. Statistical significance of Wilcoxon test (*p*-value) of the different morphological length parameters of males of *Trithemis morrisoni*, *T. palustris* and *T. stictica*. Bs: width of Hw base; A: length of outer accessory genitalia along the hamules; B: length of genital lobe; C: length of the anterior lamina; D: length of the hook of the hamule; E: width of the hamule.

	Hw	Pt-Hw	Bs-Hw	Abd	App	S4	A	B	C	D	E
stictica/palustris	0.01	0.15	0.01	0.76	0.14	0.69	0.15	0.35	0.21	0.16	0.91
stictica/morrisoni	0.00	0.11	0.00	0.00	0.02	0.00	0.00	0.33	0.10	0.08	0.87
morrisoni/palustris	0.21	0.68	0.75	0.01	0.36	0.01	0.09	0.94	0.76	0.06	1.0

the "cornuti" are curved rods which are pointed at the end, as illustrated by Pinhey (1970). The "cornuti" of *T. morrisoni* and *T. palustris* are broad in the middle and only the tip is narrower. This character is readily visible with stereomicroscopy. All 23 examined males of *T. morrisoni* and *T. palustris* show this difference with *T. stictica*. Between the two new species only slight individual variation in the "cornuti" was found (Figs 2d, e).

Statistical analyses (Wilcoxon test) of the length of the hind wing, abdomen and S4 show significant differences between the three species. In *T. stictica* the hind wings are significantly longer than in the two new species. In *T. morrisoni* the length of abdomen and S4 are significantly shorter than in *T. stictica* and *T. palustris* (Table 1). These size differences between the two new species are significantly correlated with the distinct genetic patterns (SD, HH unpubl.). Together with the fact that no overlap was observed between the species, these characters are valuable morphological characters for the populations studied here. Whether other populations might show overlaps cannot be decided yet.

All analysed individuals show the same colour pattern on thorax and abdomen, and similar external secondary genitalia as described for *T. stictica* (Figs 2a, b). Nevertheless, specimens from different geographical regions show slight differences in coloration. Specimens from Kenya, Tanzania and South Africa are black with yellow markings under the blue pruinosity, while those from Namibia appear dark brown with beige-yellow markings. This is, however, not congruent with the genetic results and can be regarded as regional intraspecific colour variation. In addition, some traits were found in a few specimens of each species. The yellow spot on S9 was found in some *T. morrisoni* and *T. stictica*, but not in *T. palustris*. The markings on the postclypeus were absent in half of the specimens of *T. morrisoni*, but present in all *T. palustris* and *T. stictica* males. In *T. palustris* these comma-shaped streaks reach to the anterior border of the postclypeus while in *T. morrisoni* and *T. stictica* only small and short commas were found. A summary of the male characters is given in Table 2.

Female morphology

The size difference between *T. morrisoni* and *T. palustris* was also found in the analysed females (Table 3). *T. morrisoni* females sampled in Zambia, are very small and have a similar size to males. The females of *T. palustris* sampled in the Okavango Delta in Botswana

Table 2. Comparison of morphological characters of males of *Trithemis morrisoni*, *T. palustris* and *T. stictica*. All measurements in [mm]. *p*-values are shown in Table 1.

	***morrisoni* (*n* = 12)**	***palustris* (*n* = 11)**	***stictica* (*n* = 20)**
Range	Okavango River and Zambezi River (Namibia, Zambia)	Okavango River and Delta, Kwando River (Botswana, Namibia)	Eastern to southern Africa
Abd length	19.9-22.5	22.7-23.8	22.1-24.8
Hw length	23.2-26.8	25.5-27.0	26.5-29.5
Pt length	3.2-3.7	3.2-3.5	3.2-3.8
Cerci length	1.3-1.6	1.5	1.2-1.7
S4 length	3.3-3.5	3.7-4.0	3.6-4.0
Wing base width	1.4-1.7	1.3-1.6	1.3-1.8
Eyes	Bicoloured	Bicoloured	Unicoloured
Wing base	Amber	Amber	Clear
"Cornuti" of penis	Broader in the middle	Broader in the middle	As described by Pinhey (1970)

Table 3. Morphological characters of the analysed females of *T. morrisoni* and *T. palustris* including the *p*-values of the statistical tests. All measurements in mm.

	***morrisoni* (*n* = 7)**	***palustris* (*n* = 7)**	***p*-values**
Locality	Zambezi River (Zambia)	Okavango Delta (Botswana)	
Abd length	20.2 – 21.5	23.5 – 24.0	0.02
Hw length	25.0 – 26.7	25.3 – 26.9	0.48
Pt length	3.2 – 3.5	3.1 – 3.5	0.70
Wing base width	1.4 – 1.6	1.5 – 1.6	0.23
S7	1.8 – 2.1	1.4 – 1.7	0.03
Colour eye underside	Yellow	Grey	
Postclypeus	Without black streaks	With black streaks	
Wing tip	Clear	Brownish	

are significantly larger (Table 3). One other character is notable: the coloration of the wings. Six of the seven *T. palustris* females from Botswana have yellow-brownish tips of the fore and hind wings, which are missing in *T. morrisoni*. Some characters were found to be species-specific in the females, but not in males. All analysed females of *T. morrisoni* have the yellow spot on S9, which is missing in *T. palustris*. However, some field-collected females of *T. palustris* do have this spot on S9 (J. Kipping pers. comm.). Therefore this difference has to be confirmed by additional sampling. The comma-shaped streaks on the postclypeus were only found in *T. palustris*, and furthermore *T. morrisoni* showed a broad S7, which is narrower in *T. palustris* (Table 3).

Habitat and distribution

Both new species were thus far only found in the region of the Okavango and Zambezi Rivers, including the Okavango Delta and Kwando River. *T. morrisoni* was collected at Andara and Popa Falls (Okavango River) and at Bovu Island (Zambezi River), while *T. palustris* was found at the mouth of the Omatako River in the Okavango River (near Rundu), the Okavango Delta, the Kwando River and also at Popa Falls (Fig. 1). *T. morrisoni* occurred at river sections with rapidly flowing water and intact gallery forest (e.g. at Popa Falls) and seemed to need at least some fast flowing side-channels of larger rivers to occur. It was absent from large and calm rivers like the Zambezi east of Lake Kariba. The main habitat of *T. palustris* appeared to be open habitats at slow flowing sections of rivers or swamps. In the Okavango Delta it was locally the most common anisopteran odonate and preferred little channels and calm rivers with swampy margins and connected floodplains. Exuviae were found at almost stagnant sections of rivers and in the nearby floodplains. It was absent from temporary flooded pans and pools. Tenerals were found in large numbers in patchy gallery forest (Kipping in press). *T. stictica* was not found in the same region although its preference for open swamps, rivers and pools (Pinhey 1970) seems to fit. In general *T. stictica* is distributed in the whole of sub-Saharan Africa (Fig.1). The Odonata Database of Africa (ODA) (J. Kipping pers. comm.) contains 537 records of this species. The westernmost records come from Sierra Leona and Liberia; in the north it occurs in Sudan, the Ethiopian highlands and Somalia. It is scarce in the mountainous parts of Central Africa and most records come from the southern countries of Zambia, Zimbabwe and South Africa. It prefers higher elevation than other members of the genus. Mean elevation of all records of *T. stictica* is 1,052 m a.s.l. ($n = 537$).

Discussion

In his monograph on the genus *Trithemis*, Pinhey (1970) described *T. stictica* as a "variable species." He studied specimens from a wide range of localities and described several regional "forms" but none of these can be clearly assigned to either of the new species. Consequently the genetic characteristic of none of Pinhey's varieties is known. He mentioned a form, possibly a subspecies, in the Okavango region with creamy or ivory faces instead of the normal yellow. We can confirm this variation in our specimens from the Okavango region, but all other analysed specimens from Namibia also show ivory instead of yellow. We regard this variation as a phenotypic rather than a diagnostic character correlated with genealogy. However, Pinhey also noted the amber base of the wings in his Okavango specimens. This character indeed distinguishes *T. stictica* from *T. morrisoni* and *T. palustris*. Pinhey also described a "dwarf series" from Victoria Falls. These specimens are relatively small and show only two rows of cells in the fore wing discoidal field. *T. morrisoni* males and females from the Zambezi River near Victoria Falls are also smaller, but all have the normal three rows of cells. Pinhey described two females of a possible Equatorial subspecies with saffronated wings and an entirely black labrum, but these features were not found in any of the analysed specimens.

Additionally, Pinhey mentioned several other variable traits in his specimens of *T. stictica*, like the yellow spot on S9, postclypeus with or without comma-shaped streaks, amber patch centrally on the hind wing absent or present, and occasionally infuscated wing tips

in the females. We found these traits in some of our specimens, but they are not species-specific. The yellow spot on S9 is absent in *T. palustris*, but was also not always present in *T. stictica* and *T. morrisoni*. The amber patch is present in most specimens of the three species, but not all. We found the darkened wing apices in six out of seven analysed females of *T. palustris*.

The status of *T. parasticta* was discussed by Pinhey (1956, 1970) and Lieftinck (1969). Pinhey (1956) described *T. parasticta* as a near ally of *T. stictica*, but larger and without the central amber patch in the hind wings. While Lieftinck (1969) confirmed its species status by comparing specimens from Lake Bangweulu with Pinhey's original description, Pinhey (1970) himself finally regarded *parasticta* merely as a larger form of *T. stictica*. We compared the diagnosis of *T. parasticta* by Lieftinck (1969) with the two new species but none of the listed traits were found. The thoracic pubescence is white as in *T. stictica* and the pterostigma has nearly the same length in all analysed individuals. Also the base of the hind wings varies only slightly in length and is smaller in *T. morrisoni* and *T. palustris* than in *T. stictica*. The superior appendages are wholly black and the yellow or amber antenodal patch on the hind wings generally exists in all three species, but varies in intensity and is absent only in some specimens. This variation is common to all three examined groups. We conclude that none of Pinhey's forms or subspecies, including *parasticta*, is one of the new species, except his possible (but unnamed) Okavango subspecies, which may have included both new species.

The genetic and morphological results support the separation of the two new species from *T. stictica* in the Okavango and Upper Zambezi Floodplains (Rach et al. 2008; SD, HH unpubl.). There are various characters to distinguish *T. morrisoni* and *T. palustris* from *T. stictica*, like the amber base of the wings, the dichromatic eyes and the structure of the penis. The latter is clearly most important due to its potential as a reproductive barrier. In addition a high sequence divergence between *T. stictica* and the two new species in four different markers (9.0% and 8.5% in ND1, 8% and 8.3% in COI, 4.5% and 4.3% in 16S and 2.0% and 2.1% in ITS, respectively) clearly separates them at the species level (SD, HH unpubl.).

The two new species cannot be identified easily in the field. However, genetic analyses clearly separate them into distinct species. We analysed 73 specimens from different sites using four genetic markers. Each sample clearly falls into only one of the two species. The sequence divergence between the two species is clearly at the species level with 5% in ND1, 5.7% in COI, 1% in 16S and 2.1% in ITS I&II (SD, HH unpubl.). A phylogenetic analysis of the genus using 37 of 40 known species corroborates the results (SD, K.-D.B. Dijkstra, HH unpubl.). Here genetic distances between other closely related species are even lower than between *T. morrisoni* and *T. palustris*, e.g. *T. donaldsoni* and *T. dejouxi* with 3.5% in ND1 or *T. grouti* and *T. aenea* with 0.6% in 16S. These levels of genetic distances were also found between other distinct odonate species, e.g. in the genera *Pseudagrion*, *Calopteryx* and *Enallagma* with the same used markers (Misof et al. 2000; Weekers et al. 2001; Turgeon & McPeek 2002; Dijkstra et al. 2007). In comparison with the study of Samraoui et al. (2003) who describe a new "cryptic" species of *Lestes* based on ITS I sequences only, we could confirm our hypothesis with four, independently inherited sequence markers. Although both species occur in the same geographical region they show high genetic distances indicative of complete reproductive isolation. The initial examination of female morphology shows that more distinguishing features may be identified in that sex, and more female samples would complement our analyses.

Interestingly, the two new species have maintained distinct genetic patterns despite a similar morphology and geographical distribution. The range of both is the Okavango and Upper Zambezi Floodplains. Nevertheless, within this region, the occupied sites differ: *T. morrisoni* was found near fast flowing water and rapids within intact gallery forest, e.g. Popa Falls and the Zambezi River near Victoria Falls. *T. palustris* was found in open areas in swamps and along slow-flowing river sections, e.g. Okavango Delta and Kwando River. The area around Popa Falls, where both species occur, provides both habitats. Because the habitat conditions differ especially for the larvae, morphological analyses of them may be a good next step. More data on the distribution and ecology of the two new species are necessary, but because they seem to occupy different ecological niches, speciation of *T. morrisoni* and *T. palustris* was most likely induced by a habitat shift (SD, HH unpubl.).

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